Morphological observations on *Oncaea mediterranea* (Claus, 1863) (Copepoda, Poecilostomatoida) with a comparison of Red Sea and eastern Mediterranean populations

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SYNOPSIS. The taxonomic status of the allegedly cosmopolitan *Oncaea mediterranea* (Claus, 1863) is reviewed. Comparison of Claus' fragmentary original description and the subsequent redescription by Giesbrecht in 1892 revealed significant differences which might lead to taxonomic confusion. Most authors have adopted Giesbrecht's identification, but it is clear that several, as yet unnamed, species have been recorded in the literature under the wrong name *O. mediterranea*. The species is redescribed in detail on the basis of material from the Red Sea and eastern Mediterranean. The occurrence of two size morphs in the eastern Mediterranean populations is briefly discussed. *O. mediterranea sensu* Bourne (1889) is regarded as *species inquirenda* in the genus.

INTRODUCTION

Oncaea mediterranea (Claus, 1863) is one of the most widely distributed oncaeids (Copepoda: Poecilostomatoida) and according to the literature assumes a cosmopolitan distribution. It has been recorded in epi- and mesopelagic layers of all three main oceans between approximately 60° N and 60° S (Malt, 1983a: Fig. 14; Heron and Bradford-Grieve, 1995). In some areas such as the offshore waters of the Lebanon (Malt *et al.*, 1989) it represents the most common oncaeid.

O. mediterranea is a well studied species. The naupliar development has been documented by Hanaoka (1952), and Malt (1983c) discussed the polymorphism and pore signature pattern of the species. Paffenhöfer (1993) obtained quantitative information on reproduction rates and longevity of adult females. It was found that early copepodids of *O. mediterranea* ingested about 100% of their body weight daily when feeding at relatively high food levels. Average reproduction rates of field-collected females ranged from 5.3 to 13.3 nauplii day^{-1}. According to Paffenhöfer (1993) neither nauplii, nor copepodids or adults of *O. mediterranea* create a feeding current, and because of their limited swimming performance the encounter with food has to be created either by motile food particles or by the copepod jumping repeatedly to locate a food-rich environment. *O. mediterranea* has been observed on discarded appendicularian houses (e.g. Alldredge, 1972) which probably serve as a major constituent of detritus and a food source for copepods in the epi- and mesopelagic zones (Ohtsuka *et al.*, 1996).

Like in many other so-called cosmopolitan planktonic species the taxonomy of *O. mediterranea* is potentially confusing. Most identifications of this species are based on the redescription of Giesbrecht (1892) from the Gulf of Naples, which was excellent by contemporary standards, and do not consider the type description of Claus (1863, as *Antaria mediterranea*) from Messina. Comparison of Claus' and Giesbrecht's text and illustrations casts certain doubts, as to whether both descriptions are based on the same species. As part

of an ongoing study on Red Sea oncaeids the taxonomic history of *O. mediterranea* is reviewed and the species is redescribed herein on the basis of material from the eastern Mediterranean and various regions in the Red Sea.

METHODS

Oncaeids were collected using a multiple opening-closing net with a mesh size of 0.05 mm during cruise 5/5 of R/V *Meteor* in the Southern and Central Red Sea and in the Eastern Mediterranean Sea. A station list and sampling data are given in Table 1. The plankton was initially fixed in 4% formaldehyde-seawater solution buffered with hexamethylene tetramine and transferred after ca 2 years into a preservation fluid of 5% propylene glycol, 0.5% propylene phenoxetol, and 94.5% filtered seawater (Steedman, 1976). Specimens were dissected in lactic acid, and mounted on slides in lactophenol. All figures have been prepared using a camera lucida on a Leitz Dialux differential interference contrast microscope.

Total body length and the ratio of prosome to urosome (excluding caudal rami) were calculated as the sum of the middorsal lengths

Table 1 Station data of sampling with 0.05 mm mesh multiple opening closing net during R/V *Meteor* Cruise 5.

Stn. No.	Haul No.	Date (1987)	Time	Latitude (°N)	Longitude (°E)	Depth of Haul (m)	Total water depth (m)
Red Sea							
663	17/4	20.07	Day	22°58.4'	37°19.4'	50–100	1200
703	39/5	03.08	Day	15°34.8'	41°54.9'	0–50	970
	39/4					50–100	
Eastern Mediterranean							
44	31/5	24.01	Day	34°07.1'	31°54.7'	0–50	2530

of individual somites measured in lateral view. In the case of telescoping somites these lengths are measured from the anterior to the posterior margin. This approach differs from that traditionally used in oncaeid taxonomy, where the telescoping of somites is not considered in length measurements. Thus, sizes of the species in this paper are not directly comparable to those of previous descriptions (e.g. Heron, 1977; Heron and Bradford-Grieve, 1995) or earlier studies in the Red Sea (Böttger-Schnack et al., 1989). Length data given by the latter authors are only about 70% of the length presented in this paper, due to the excessive telescoping of somites in the sorting medium.

Descriptive terminology for body and appendages follows that of Huys and Boxshall (1991). Abbreviations used in the text are: ae = aesthetasc; CR = caudal rami.

SYSTEMATICS

Order **POECILOSTOMATOIDA** Thorell, 1859
Family **ONCAEIDAE** Giesbrecht, 1892
Genus *ONCAEA* Philippi, 1843

Oncaea mediterranea (Claus, 1863)

(Figs 1–5)

SYNONYMS. *Antaria mediterranea* Claus, 1863; *Oncæa mediterranea* (Claus, 1863); *Oncäa mediterranea* (Claus, 1863).

ORIGINAL DESCRIPTION.   Claus (1863): 159–160, Tafel XXX, Fig. 1–6 (♀), 7 (♂).

OTHER DESCRIPTIONS.   Giesbrecht (1892) [as *Oncäa mediterranea*]; Heron (1977) and Heron & Bradford-Grieve (1995) [as *Oncaea mediterranea*].

TYPE LOCALITY.   Tyrrhenian Sea; Messina.

MATERIAL EXAMINED. (see Table I for locality data)

(1)   The Natural History Museum, London: Southern Red Sea: Stn 703; R/V *Meteor* leg 5/5; collected with MSN 0.05 mm net (Haul 39/4); depth 50–100 m: 10♀♀ and 10♂♂ in alcohol (reg. nos 1996.1095–1114); leg. R. Böttger-Schnack;
(2)   Dr Böttger-Schnack (personal collection):
    (a) Southern Red Sea: Stn 703; R/V *Meteor* leg 5/5; collected with MSN 0.05 mm net (Haul 39/4); depth 50–100 m; leg. R. Böttger-Schnack: several♀♀ and ♂♂ in alcohol;
    (b) Central-Northern Red Sea: Stn 663; R/V *Meteor* leg 5/5; collected with MSN 0.05 mm net (Haul 17/4); depth 50–100 m; leg. R. Böttger-Schnack: several♀♀ and ♂♂ in alcohol;
    (c) Eastern Mediterranean: Stn 44; R/V *Meteor* leg 5/1; collected with MSN 0.05 mm net (Haul 31/5); depth 50–100 m; leg R. Böttger-Schnack: (i) small form: 1♀ and 1 ♂ dissected on slides, 1♀ in alcohol; (ii) broad form: 2 ♀♀ dissected on slides, 1♂ in alcohol.

ADULT FEMALE
Body length (measured in lateral aspect; from anterior margin of rostral area to posterior margin of caudal rami, calculated as sum of individual somites): 1400 μm
Exoskeleton well chitinized. Prosome 2.2 times length of urosome, excluding caudal rami, 1.9 times urosome length including caudal

rami. Leg 2-bearing somite without conspicuous dorso-posterior projection (Fig. 1B). Leg 3-bearing somite with conspicuous raised pore protruding laterally (Fig. 1a). Other integumental pores on prosome as indicated in Fig. 1A–B. Pleural areas of leg 4-bearing somite with constricted posterolateral corners.

Proportional lengths (%) of urosomites are 9.7 : 60.7 : 8.2 : 8.8 : 12.6. Proportional lengths (%) of urosomites and caudal rami are 8.1 : 50.7 : 6.8 : 7.3 : 10.5 : 16.5.

Genital double-somite nearly twice as long as maximum width (measured in dorsal aspect) and twice as long as postgenital somites combined; largest width measured at anterior third, posterior part tapering gradually. Paired genital apertures located at about halfway the distance from anterior margin of genital double-somite; armature represented by 1 spine and 1 diminutive spinule (Fig. 1H). Pore pattern on dorsal surface as indicated in Fig. 1C.

Anal somite 1.3 times wider than long; about 2/3 the length of caudal rami (Fig. 1C). Secretory pore discernible on either side of anal opening. Anterior margin of anal opening (vestigial anal operculum) with transverse row of minute denticles. Posterior margin of somite finely serrate ventrally and laterally (Fig. 1D).

Caudal ramus (Fig. 1F) about 3.0 times as long as wide. Armature consisting of 6 elements: antero- and posterolateral setae long, spiniform and unipinnate along medial margin; outer terminal seta long and plumose; inner terminal seta longest and plumose; terminal accessory seta more than 2/3 the length of outer terminal seta and more than twice the length of caudal ramus; dorsal seta about half the length of terminal accessory seta, plumose and bi-articulate at base. Inner margin of somite with fringe of long, setules. Dorsal anterior surface (Fig. 1F) with secretory pore near insertion of seta II. Dorsal surface covered with numerous small scales (Fig. 1F).

Antennule 6-segmented (Fig. 1E), relative lengths (%) of segments measured along posterior non-setiferous margin 6.2 : 20.6 : 46.4 : 10.3 : 6.2 : 10.3. Armature formula: 1-[3], 2-[8], 3-[5], 4-[3+ae], 5-[2+ae], 6-[6+(1+ae)].

Antenna 3-segmented, distinctly reflexed (Fig. 2A). Coxobasis with row of long, fine spinules or setules along outer and inner margins and with few additional spinules on proximal and distal part of outer (exopodal) margin; with bipinnate seta at inner distal corner. Endopod segments unequal in length; proximal endopod segment subtriangular forming outer lobate outgrowth bearing spinular patch, with row of denticles along posterior inner margin. Distal endopod segment slightly shorter than proximal exopod segment, with narrow cylindrical base articulating; with two patches of short spinules along outer margin; lateral armature consisting of 1 unipinnate spiniform seta and 3 curved setae, one of them sparsely pinnate, all armature elements similar in length; distal armature consisting of 5 long unipinnate setae and 2 short naked setae; none of armature elements spiniform or geniculate.

Labrum (Fig. 2B–C) distinctly bilobed. Distal margin of each lobe with 4 strong dentiform processes medially, short row of long fine setules latero-distally and row of minute spinules laterally. Lobes separated by semicircular vertex covered anteriorly by overlapping rows of hyaline petaloid flaps. Posterior part of medial incision with four rounded integumental thickenings. Anterior surface (Fig. 2B) with short row of spinules either side of median swelling, raised row of small strong denticles latero-posteriorly; median swelling with large secretory pore posteriorly. Posterior surface (Fig. 2C) with group of 3 secretory pores located on proximal part of each lobe and an additional one basally.

Mandible (Fig. 2D) with minute spinules on surface of coxa; gnathobase with 5 elements: 1 at subdistal ventral corner, 2 along distal margin and 2 along subdistal dorsal margin; ventral element shorter than ventral blade, with long, fine setules along dorsal
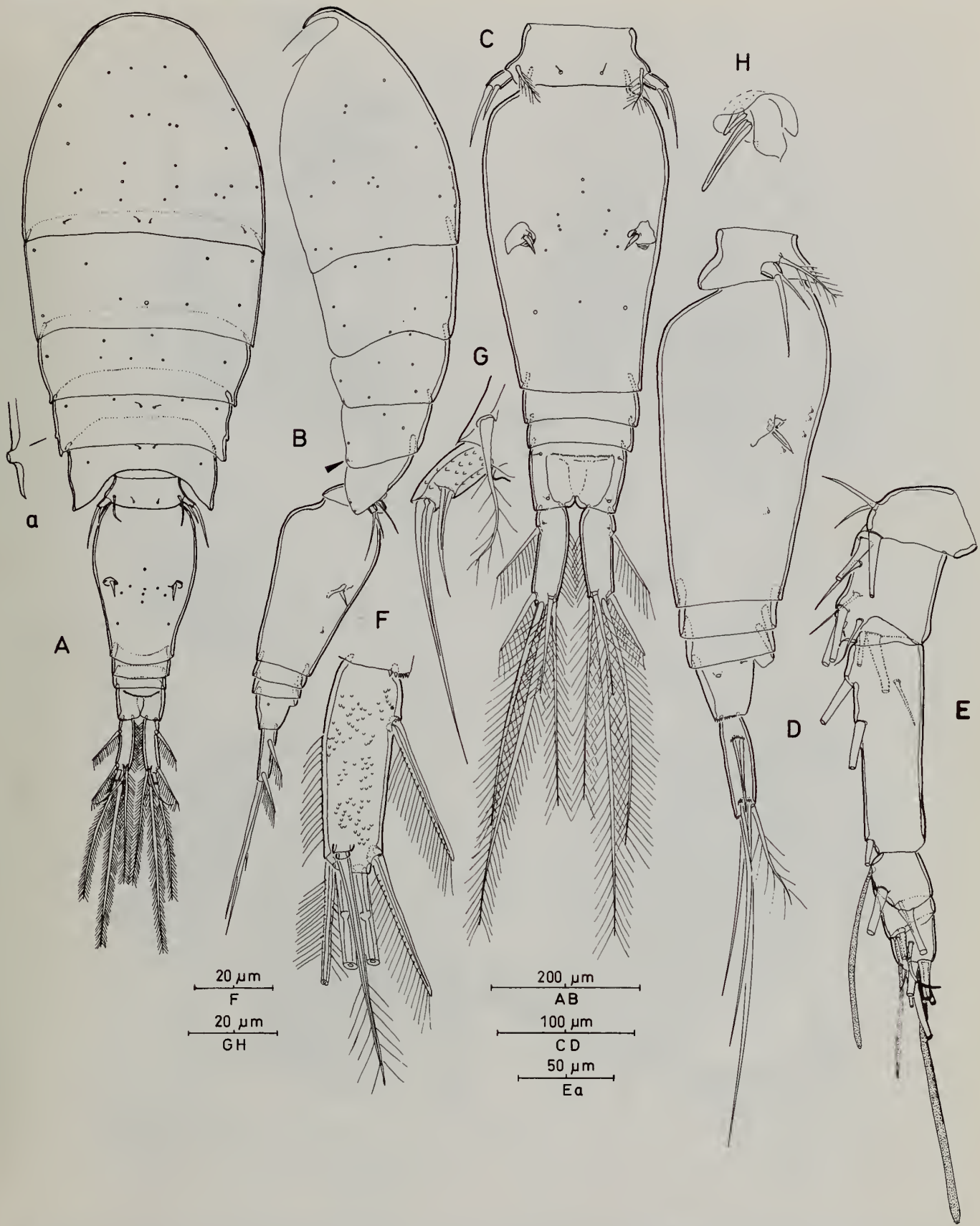
Fig. 1 *Oncaea mediterranea* (Claus, 1863), ♀ (Red Sea). A, habitus, dorsal [a: lateral raised pore, enlarged]; B, same, lateral (appendages omitted), arrow indicating position of lateral raised pore; C, urosome, dorsal; D, urosome, lateral; E, antennule; F, caudal ramus, dorsal; G, leg 5, dorsal; H, leg 6.
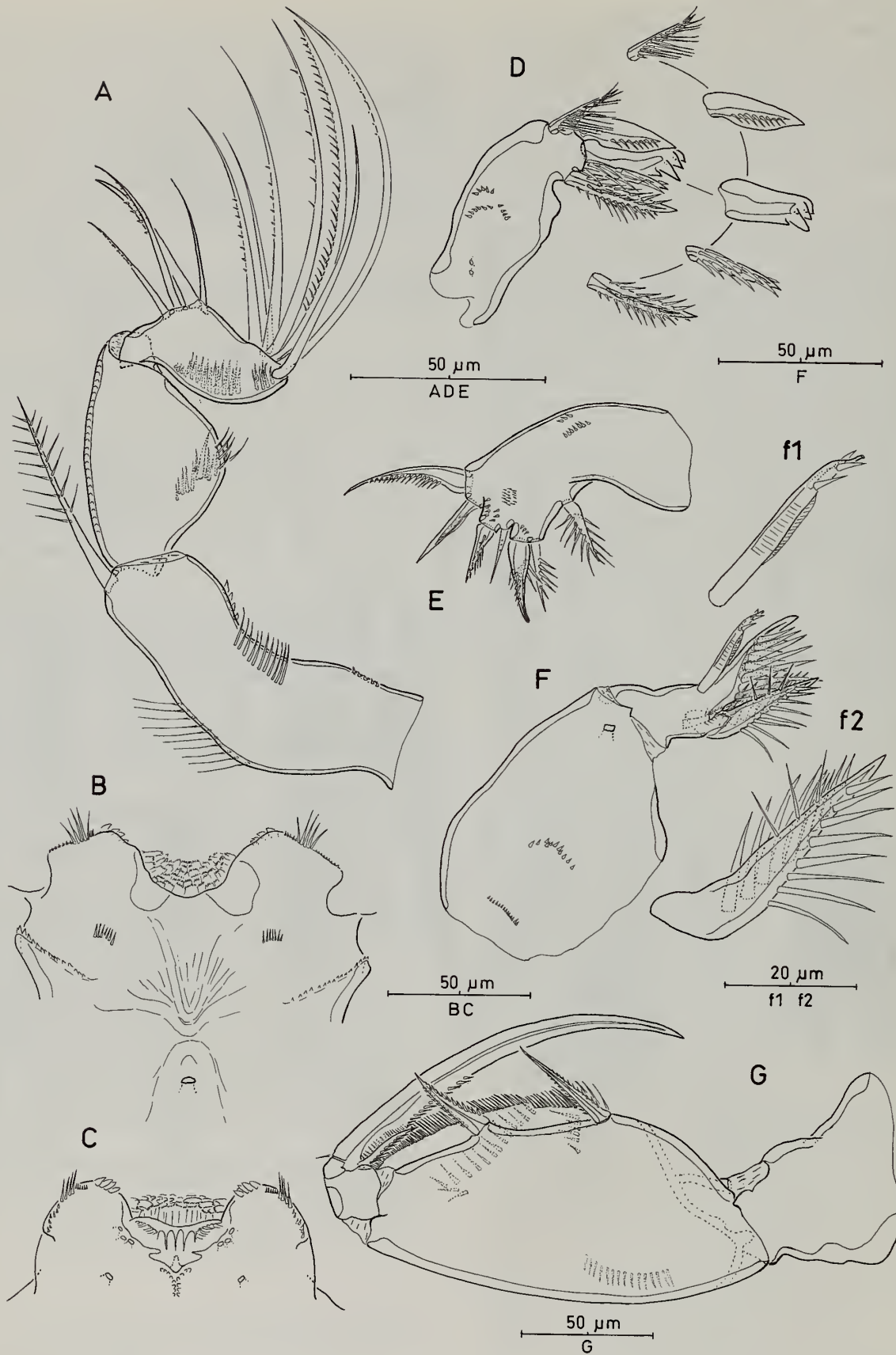
Fig. 2 *Oncaea mediterranea* (Claus, 1863), ♀ (Red Sea). A, antenna; B, labrum, anterior; C, same, posterior; D, mandible, showing individual elements; E, maxillule; F, maxilla, [f1, distal seta; f2, proximal seta]; G, maxilliped.
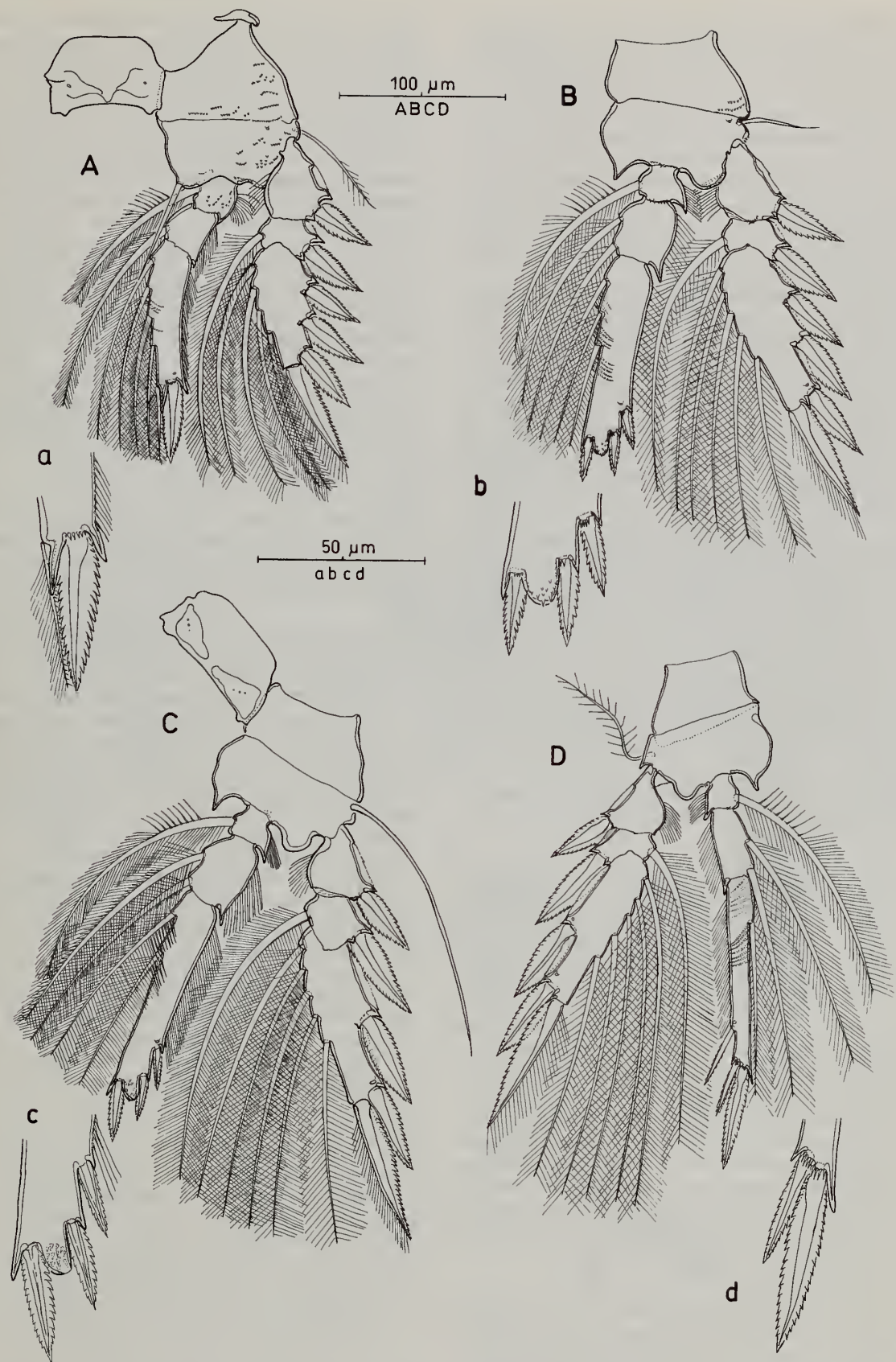
Fig. 3 *Oncaea mediterranea* (Claus, 1863), ♀ (Red Sea). A, leg 1, anterior [a, terminal part of endopod]; B, leg 2, anterior [b, terminal part of endopod];
C, leg 3, posterior [c, terminal part of endopod]; D, leg 4, anterior [d, terminal part of endopod].

margin; ventral blade strong and spiniform, with row of setules on posterior surface; dorsal blade strong and broad, with four dentiform processes around distal margin; dorsal elements setiform, the shorter hyaline, flat and densely setose, the longer multiipinnate.

Maxillule (Fig. 2E) indistinctly bilobed, with numerous spinules on anterior and posterior surfaces. Inner lobe subcylindrical, with 3 elements: outermost one spiniform, swollen at base, fringed with coarse spinules, others setiform and bipinnate; innermost one located along concave inner margin at some distance from other elements. Outer lobe with 4 elements; outermost element spiniform, curved and unipinnate, longer than the following; other elements with sparse spinules, innermost one shortest.

Maxilla (Fig. 2F) 2-segmented, comprising syncoxa and allobasis. Syncoxa unarmed, surface ornamented with 2 spinular rows and 1 large secretory pore. Allobasis produced distally into slightly curved claw bearing 2 rows of very strong spinules along medial margin; outer margin with strong seta almost extending to tip of allobasal claw, ornamented with few strong spinules distally and a thin hyaline lamella bilaterally, tip of seta with tubular extension (Fig. 2f1); inner margin with slender pinnate seta and strong basally swollen spine with double row of very strong spinules along the medial margin and single row of shorter spinules along outer margin (Fig. 2f2).

Maxilliped (Fig. 2G) 4-segmented, comprising syncoxa, basis and 2-segmented endopod. Syncoxa unarmed, without surface ornamentation. Basis robust, inner margin with 2 spiniform bipinnate elements nearly equal in length; fringe of long pinnules between proximal seta and articulation with endopod; two rows of long setules on anterior surface as illustrated in Fig. 2G. Proximal endopod segment unarmed. Distal endopod segment drawn out into long curved claw, with pinnules along proximal half of concave margin; accessory armature consisting of minute, naked seta on outer proximal margin and unipectinate spine fused basally to inner proximal corner of claw.

Swimming legs 1–4 biramous (Fig. 3A–D), with 3-segmented rami. Spine and setal formulae as follows:

	Coxa	Basis	Endopod	Exopod
Leg 1	0–0	1–I	0–1; 0–1; 0,I,5	I–0; I–1; III,I,4
Leg 2	0–0	1–0	0–1; 0–2; I,II,3	I–0; I–1; III,I,5
Leg 3	0–0	1–0	0–1; 0–2; I,II,2	I–0; I–1; II,I,5
Leg 4	0–0	1–0	0–1; 0–2; I,II,1	I–0; I–1; II,I,5

Intercoxal sclerites well developed, without ornamentation. Coxae and bases of legs 1–3 with surface ornamentation as shown in Fig. 3A–C. Bases with plumose (legs 1, 4), short naked (leg 2) or very long naked, outer seta (leg 3); with anterior secretory pore near outer proximal corner; inner portion slightly produced adaxially in legs 2–4 (Fig. 3B–D). Inner basal seta on leg 1 long, spiniform and naked. Respective legs without distinct length differences between rami with endopod slightly longer than exopod. Bases of spines on exopodal and endopodal segments surrounded by small spinules which are most obvious around terminal endopod spines of legs 2 and 4 (Fig. 3b,d). Surface ornamentation of all segments with small scales, similar to those on caudal ramus (Fig. 1F).

Exopods. Outer margin of exopod segments with well developed serrated hyaline lamella; inner margin of proximal exopod segments with long setules. Secretory pore present on posterior surface of distal segments. Hyaline lamellae on outer exopodal spines well developed. Terminal spine of leg 1 equal in length to (leg 1) or shorter than (legs 2–4) distal exopod segment.

Endopods. Outer margin of endopod segments with fringe of long setules. Inner seta of proximal endopod segment slightly swollen. Distal endopod segments with single secretory pore on posterior surface; distal margin of legs 2 and 3 produced into conical projection ornamented with minute spinules anteriorly (Fig. 3B,C,b,c). Outer subdistal spine equal in length to distal spine in legs 2–4. Outer margin of distal segment of leg 1 terminating in a long process obscuring insertion of distalmost inner seta (Fig. 3a). Inner setae of distal endopod segments of legs 2–4 with spinule comb along proximal inner margin; this comb less obvious in leg 1; also present on distal inner seta of middle endopod segment in leg 4.

Leg 5 (Fig. 1G) comprising small plumose seta arising from lateral surface of somite, and small free segment representing exopod. Exopod slightly longer than wide, bearing stout curved seta apically and smaller slender seta inserted subdistally; surface covered with minute denticles

Leg 6 (Fig. 1C, H) represented by operculum closing off each genital aperture; armed with a spine and a short spinule.

Egg-sacs paired, oval-shaped; each sac containing approximately 40 eggs (diameter 50–65 μm).

ADULT MALE
Body length (measured in lateral aspect; from anterior margin of rostral area to posterior margin of caudal rami, calculated as sum of individual somites): 960 μm. Sexual dimorphism in antennule, antenna, maxilliped, legs 5–6, caudal ramus and in genital segmentation.

Proportional lengths (%) of urosomites (excluding caudal rami) 9.4 : 70.0. : 3.4 : 3.8 : 3.0 : 10.5 ; proportional lengths (%) of urosomites (caudal rami included) 8.4 : 62.1 : 3.0 : 3.3 : 2.7 : 8.1 : 11.6. Leg 5-bearing somite with transverse row of denticles dorsally (Fig. 4D). Caudal rami 1.8 times longer than wide, markedly shorter than in female. Caudal setae with proportional lengths as in female. Dorsal surface of genital somite covered with scale-like structures in anterior half, arranged in a specific pattern (not figured). Surface of genital flaps and ventral surface of anal segment ornamented with several rows of small spinules (Fig. 4E). Dorsal surface of caudal ramus covered with minute scales as in female.

Antennule (Fig. 4B) 4-segmented; distal segment corresponding to fused segments 4–6 of female; relative lengths (%) of segments measured along posterior non-setiferous margin 14.5 : 19.7 : 42.1 : 23.7. Armature formula: 1-[3], 2-[8], 3-[4], 4-[11+2ae+(1+ae)].

Antenna as in female, except for lateral armature on distal endopod segment (Fig. 4G), with third spiniform element being much stouter than in female and shorter than the 2 adjacent setae.

Maxilliped (Fig. 4C) 3-segmented, comprising syncoxa, basis and 1-segmented endopod. Syncoxa without surface ornamentation, unarmed. Basis robust, particularly inflated in proximal half forming bulbous swelling; anterior surface with 2–3 transverse spinular rows in addition to row of short flat spinules along inner margin (Fig.4C); posterior surface with 3 rows of short spatulated spinules of graduated length along palmar margin (Fig. 4C); with 2 small naked setae inserted within the longitudinal cleft, the proximal one being slightly longer than the distal one. Endopod drawn out into long curved claw, concave margin unornamented; accessory armature consisting of short, unipectinate spine basally fused to inner proximal corner of claw; claw with minute hyaline apex (Fig. 4c).

Legs 1–4 with armature as in female; variable number of spinules on conical projection of endopods of legs 2 and 3.

Leg 5 (Fig. 4D, F) exopod not delimited from somite, general shape and armature as in female; small plumose seta arising from lateral surface of somite as in female.

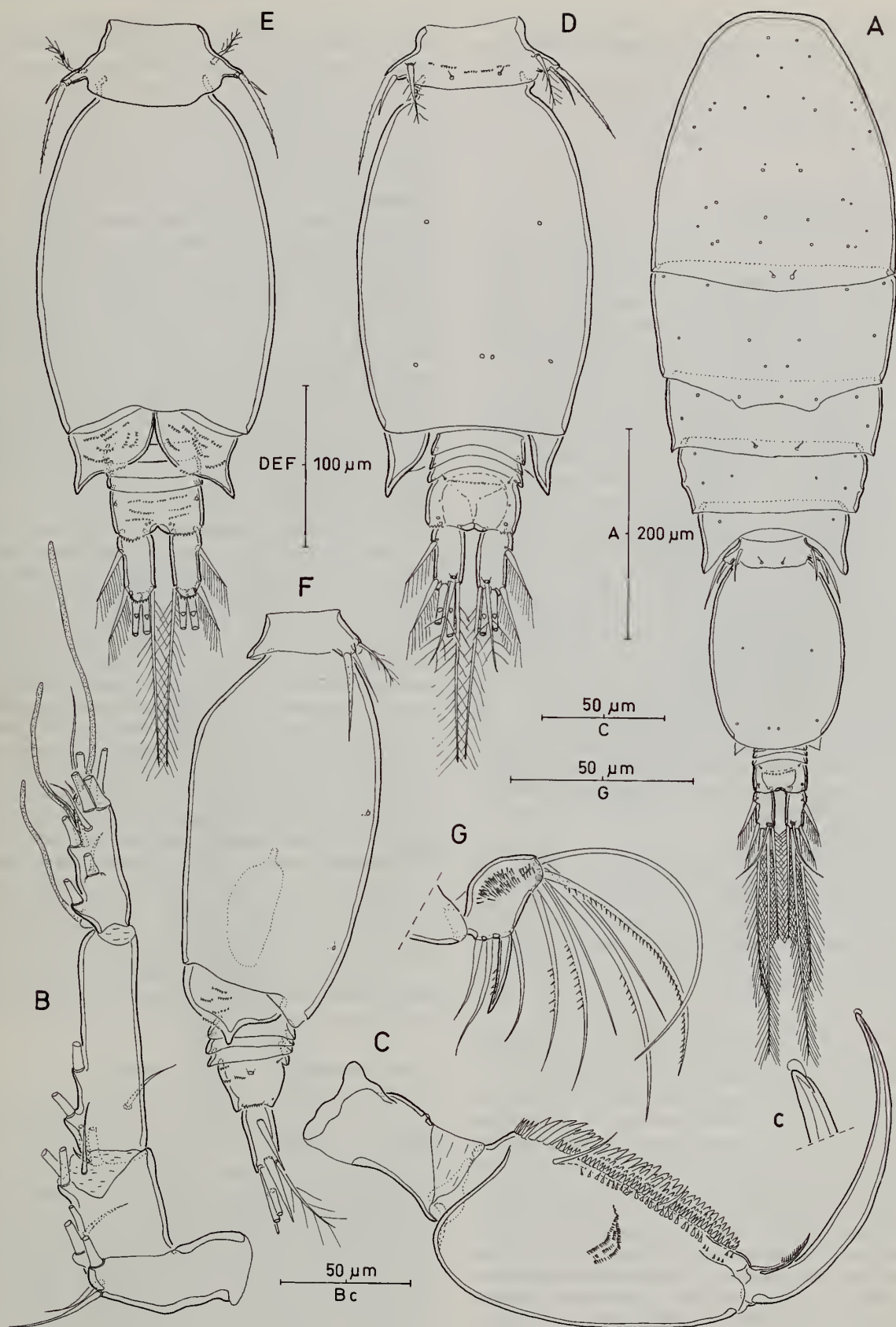Leg 6 (Fig. 4E) represented by posterolateral flap closing off

Fig. 4 *Oncaea mediterranea* (Claus, 1863), ♂ (Red Sea). A, habitus, dorsal; B, antennule; C, maxilliped, anterior [c, tip of claw, showing hyaline lamella]; D, urosome, dorsal; E, urosome, ventral; F, same, lateral (spermatophores immature); G, antenna, distal endopod segment.

genital aperture on either side; covered by pattern of denticles as shown in Fig. 4E; posterolateral corners protruding laterally so that they are discernible in dorsal aspect (Fig. 4D).

Spermatophore oval, of variable size according to state of maturity (Fig. 4F); swelling of spermatophore during development not affecting shape or relative size of genital somite.

TAXONOMIC HISTORY

Claus (1863:159) presented a concise original description of *Antaria mediterranea* with some illustrations of both sexes. Later Claus (1866) identified two size groups upon re-examination of original material from Messina: the large one [1.3 mm excluding CR setae] being the one that was mentioned in the original description; the small one [0.8–0.9 mm] which he also recorded from Nice; no overlap was found between both size morphs from Messina.

Lilljeborg (1875) recorded a single specimen from Mosselbay (Spitsbergen), and Car (1884) found it in plankton samples taken off Trieste in the Adriatic Sea. Both authors, however, gave no descriptions or figures and their records therefore remain unconfirmed.

Bourne (1889) [as *On[c]æa mediterranea*] found 2 females in surface waters off Plymouth. Giesbrecht (1892) regarded this record doubtful and pointed out the discrepancy between the text and figures with regard to the CR/anal somite length ratio. Careful comparison of this character is hampered by the fact that Claus (1863) only figured the female in lateral aspect and by the possibility that the urosome is considerably telescoped in the specimen illustrated by Bourne. Giesbrecht's statement that Bourne's and Claus' specimens differ fundamentally in maxilliped structure is equivocal since he compared the former with what he had identified as *O. mediterranea* rather than with the original type material. On the basis of Brady's (1883) illustrations [Challenger Expedition], Bourne (1889) also tentatively regarded *Onc[æ]a obtusa* (Dana) as a possible synonym of *O. mediterranea*, however, as Giesbrecht (1892) and subsequent authors suspected, the latter could as well be conspecific with *O. venusta* Philippi.

Giesbrecht (1892) reviewed the earlier literature on *Antaria* and *Oncaea*, and summarized the synonymies of the respective species known at that time. Dana's (1849) species *Antaria obtusa* and *A. crassimana* were included under the synonymy of both *O. venusta* and *O. mediterranea*, reflecting the author's undecisiveness on this matter. Giesbrecht redescribed *O. mediterranea* on the basis of material from Naples and distinguished two colour varieties *flava* and *rubra*.

Comparison of Giesbrecht's illustrations with Claus' original description, however, raises some doubts as to the conspecificity of the Messina and Naples specimens. The major obstacle in this comparison lies in the form, position and size of the setae on the maxillipedal basis which is usually considered as an important discriminant in oncaeid systematics. The issue is even more complicated by the discrepancy between text and figures in Claus' original description. Claus (1863) stated that there are two ornated setae on the palmar margin of the basis, yet in his figure (Tafel XXX, Fig. 6) only one naked seta is illustrated. From the position of this seta, being located halfway the inner margin, it is conceivable that Claus has overlooked the proximal seta. This hints at the possibility that Claus' *O. mediterranea* is related to the 'englishi species-group' which includes *O. ornata* Giesbrecht, 1891, *O. shmelevi* Gordejeva, 1972, *O. englishi* Heron, 1977 and *O. alboranica* Shmeleva, 1979. In these species the distal element is long, slender and minutely pinnate, whereas the proximal one is spiniform and because of its

small size easily overlooked or misinterpreted as a spinule. In Giesbrecht's *O. mediterranea*, however, both elements are (1) of about the same size and only half the length of the proximal seta in the Messina material, and (2) positioned differently, i.e. the proximal one at 1/3 distance from the syncoxa-basis joint, the distal one at 2/3 distance. A second possibility is that the long palmar seta in Claus' original illustration is in fact a maxillary element superimposed on the maxilliped since Claus believed that both appendages represented the rami of a single limb, i.e. the maxilliped.

Other differences are found in the female leg 5 which is longer in the original description and the shape of the genital double-somite in lateral aspect which does not have the pronounced swelling anterioventrally as shown in Giesbrecht's illustration (Taf. 4, Fig. 16). The male of Claus' *O. mediterranea* shows an exceptionally long leg 5 exopod (his Taf. XXX Fig. 7) which might or might not be free. This character has thus far been found in only a small number of *Oncaea* species belonging to the *notopus* group, such as *O. damkaeri* Heron, 1977 and *O. parila* Heron, 1977 (Heron, 1977; Heron *et al.*, 1984) which also display a very long leg 5 exopod in the females. Species of the *notopus* group have a setation pattern on the female maxilliped which is significantly different from that displayed in the *englishi* group which raises the suspicion that Claus (1863) might well have based males and females on different species.

As a result of this comparison it is clear that Claus' original text and drawings contain several internal inconsistencies and lack the detail that is necessary to allow unequivocal identification. The setation of the maxilliped is a potentially critical character in this process as confirmation or refutal of Giesbrecht's identification depends on whether more weight is given to the text statement or to the illustration. Given the fact that Claus' figures of the other cephalic appendages are similarly poor (setation elements are missing from every limb) it is preferred here to give more weight to the text as this will lead to nomenclatural stability. Pending the rediscovery of Claus' types (which are in all probability lost) this admittedly subjective decision is the best course of action. In view of the grossly fragmentary original description in which the sexes were based on two different – but unidentifiable – species and in the absence of formal holotype designation the taxonomic problem is in our opinion unsolvable. Moreover, it is considered highly unlikely that collection of topotype material from Messina would be informative as 130 years have lapsed since Claus' discovery of the species in an open pelagic environment that might have been subjected to major changes since, such as the opening of the Suez Canal in 1869.

O. mediterranea (Claus, 1863) *sensu* Bourne (1889) is clearly different from the Mediterranean material and is regarded here as *species inquirenda* in the genus.

Other records of *O. mediterranea*.

O. mediterranea has been recorded from a wide range of localities such as the Antarctic (Heron, 1977) and the Red Sea (Böttger-Schnack, 1988). Many of its records, however, remain unconfirmed such as the Red Sea records of Cleve (1900, 1903) and Thompson and Scott (1903) [compiled by Halim (1969)]. Since most authors have followed Giesbrecht's identification and ignored Claus' original description it is likely that at least one, as yet unnamed, species became established in the literature under the wrong name *O. mediterranea*. For example, re-examination of material collected during the *Terra Nova* and *Challenger* expeditions (deposited in The Natural History Museum) proved to belong to at least two distinct species differing in several aspects from *O. mediterranea*. Scott (1894) recorded this species ('1 or 2 females') from the Gulf of Guinea, but re-examination of his illustrations leave little doubt that
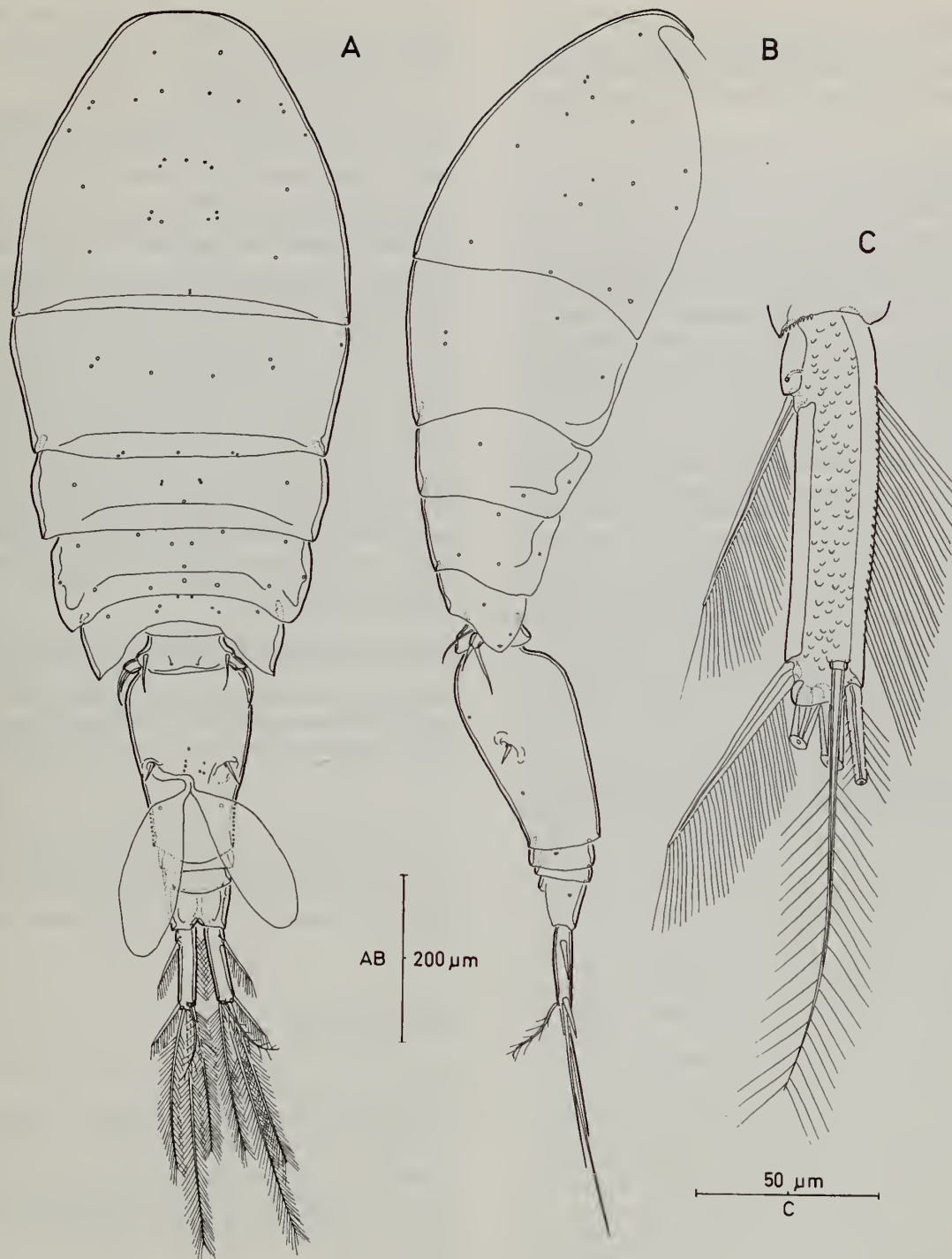
A

B

C

AB 200 µm

50 µm
C

Fig. 5 *Oncaea mediterranea* (Claus, 1863), ♀, broad form (eastern Mediterranean). A, habitus, dorsal; B, same, lateral; C, caudal ramus.

he was dealing with a species of the *englishi* group. Supporting evidence for this is found in the morphology of the antenna, maxilliped and leg 4. Dakin and Colefax (1940) recorded the species from New South Wales from a depth of 0–200 m were it was 'rare' but it is doubtful whether they were dealing with *O. mediterranea* since material collected from the Great Barrier Reef and identified with Claus' species proved upon re-examination to belong to a closely related undescribed species. Razouls (1974) described *O. mediterranea* from the region of Banyuls-sur-mer (Golfe du Lion) and summarized previous records from the Mediterranean Sea. His

drawing (Fig. 4G) of the male shows a terminal conical projection on the endopod of swimming leg 4 which disproves his identification as this is a character exclusively found in representatives of the *conifera-similis* complex. Ferrari (1973, 1975) recorded the species from the Gulf of Mexico and the northern Caribbean Sea and distinguished three size variants, the status of which will be discussed below under 'form variants' of *O. mediterranea*. Boxshall (1977a) recorded *O. mediterranea* from the Northeastern Atlantic near the Cape Verde Islands and in another report (Boxshall, 1977b) gave detailed information on their vertical distribution and diurnal vertical migration.

Many more records of *O. mediterranea* from different localities in the world ocean are known [see Malt (1983a) for a review], but are not considered here, because they did not include figures or a description that positively identified the species.

FORM VARIANTS

In the eastern Mediterranean, *O. mediterranea* exhibits two forms in both sexes: a smaller and more slender form and a larger, more robust form. These forms differ only in the general appearance and in the length : width ratio of the caudal ramus in the females. The difference in general habitus between the two is caused by the greater width of the leg 2-bearing and leg 3-bearing somites in the larger form (Fig. 5A). In the females, the length to width ratio of the caudal rami is larger in the broad form (4:1) (Fig. 5C) as compared to the small form (3:1, cf. Fig. 1F), whereas in the males no corresponding difference could be found. No other morphological differences were discernible between the two morphs. The small form of *O. mediterranea* corresponds to the small variant described by Malt (1983a), while the large form seems to be similar to her 'typical' *mediterranea* form. Only one size morph of *O. mediterranea* was found in the Red Sea, which can be identified as the small form found in the eastern Mediterranean and on the basis of the length to width ratio of caudal rami seems to resemble the small form of *O. mediterranea* recognized by Malt (1983b). A small colourless form of *O. mediterranea* (in addition to the larger 'orange-golden' form) was found south of New Zealand by Farran (1929) but no further description was provided.

Ferrari (1975) reported the existence of three distinct size groups in *O. mediterranea* of the Gulf of Mexico. The two larger forms differed only in size, but had a similar length to width ratio of the caudal ramus of 4:1. On the basis of their morphometry they might be assigned to the typical form of *O. mediterranea* (*sensu* Malt). The smaller size group had a length to width ratio of the caudal ramus of 3.0–3.5:1 and might thus be similar to the small form *sensu* Malt and to that found in the Red Sea. The smaller morph was initially regarded as a potential new species (Ferrari, 1973) since it differed both in the proportional lengths of body somites as well as in total body size. Subsequently, Ferrari (1974), quoting *O. conifera* Giesbrecht, 1891 as an exemplar of gross relative size variation in oncaeids, considered it as merely another size group of *O. mediterranea* since not structural differences could be detected in the appendages. The recent outstanding work on the *conifera*-complex by Heron and Bradford-Grieve (1995) has amply demonstrated that much of the 'variation' in *O. conifera* can be explained by the fact that morphologically similar species can co-exist and that this morphological similarity can even cause anomalies in the mate guarding configurations of certain species. It is conceivable that many of the form variants represent genuine species which can no longer be discriminated using traditional α-taxonomical methods. For example, Malt (1983c) mapped the pore signature pattern of the two female forms of *O. mediterranea* from the North Atlantic but failed to reveal any significant difference between them. It seems therefore that the question whether the large morph found in the Eastern Mediterranean represents a sibling species of *O. mediterranea* can perhaps only be resolved by breeding experiments or alternative methods using molecular data such as enzyme electrophoresis, immunological distance methods or ribosomal RNA sequencing.

ECOLOGICAL NOTES

Geographical distribution.

O. mediterranea is distributed throughout the Red Sea (see review in Halim (1969); Böttger-Schnack, 1990b, 1995). It was also found in small mesh net samples from the northernmost part of the Gulf of Aqaba (Böttger-Schnack, unpubl.).

Vertical distribution and vertical migration.

During summer and autumn, when a strong seasonal thermocline is developed, the core of the *O. mediterranea* population during the day is situated in the zone below the thermocline, at 50–150 m (Böttger-Schnack, 1990a, unpubl.). Parts of the population migrate into the upper 50 m during the night, with males showing a greater proportion of migrating individuals than females. For females, a bimodal vertical distribution can be found during these seasons, with the lower part of the population dwelling in the 250–400 m layer, in the core of the oxygen minimum zone. In the northern Red Sea the mesopelagic populations of females are found at greater depths than in the central area, corresponding to the regional differences in the depth of minimal oxygen concentrations (Böttger-Schnack, 1990b). These deep dwelling populations are not found during winter (Böttger-Schnack, 1990b).

Seasonal variation in abundance (central Red Sea).

No consistent seasonal variation in abundance was found for *O. mediterranea* in the central Red Sea, indicating that the populations are not substantially recruited by those from the south (Böttger-Schnack, 1995).

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